# THE MALE RECEPTACLE AND ANTHERIDIUM OF *REBOULIA HEMISPHAERICA*

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The genus Reboulia has received less attention from morphologists than certain other forms of the Marchantiales, although recent papers by C. and R. Douin (10), Woodburn (29), and Haupt (16, 17) give evidence of a present interest in the form. The writer has shared in this interest and for some time has had in progress a study of *R. hemisphaerica* (L.) Raddi with a view to securing as complete an account of its morphology as a large collection of material would afford. The results of the writer's study of the origin and structure of the air chambers have been recently presented (11). Haupt's account is the only critical study of the sex organs to date, and should receive due credit as such. The following account of the antheridial structures confirms the work of Haupt in some features and supplements it in others.

The material used in this study was for the most part collected from the lower margins of a north-exposed talus slope at the base of a steep shale cliff, near Huntingdon, Pennsylvania, at intervals from 1912 to 1920. A second group of material was secured from near Mount Carroll, Illinois, in January, 1916, and kept in good growing condition in the botanical greenhouse of the University of Chicago. The last collection from this material was made in August, 1916. Under field conditions antheridia develop during the latter part of the summer, especially in August. In the greenhouse cultures antheridia were forming as early as April, although the August collections also showed antheridial receptacles in early stages of development.

## Historical

The early study of Reboulia was concerned with its taxonomic features. Micheli (24) gave good figures of the male disc, describing the plant as "*Hepatica media capitulo hemispherico*." Bischoff (1) noted the median or terminal position of the flat receptacle and the erect antheridia imbedded within its tissue. Hofmeister (18) observed the mature antheridium, claiming the tabular wall to be supplanted toward maturity by a membranous sac. He cites and figures the male receptacle directly behind the female receptacle. His suggestion that it is "probable that these [antheridial] cushions may be weakly developed shoots" is of interest. Leitgeb (21, 22) regarded the receptacle as a dorsal outgrowth, not involving the thallus apex in its formation, but in cases when the apex is permanently checked the receptacle appears terminal. He found that the thallus usually renews growth and may produce one or more successive discs. Leitgeb agrees with Nees ab Esenbeck (25) that the female receptacle is near the male but on a different branch, the thallus forking just before sex-organ formation and the one fork producing a male, the other a female receptacle, although both forks may produce the same sex organs. He gives no case in which both receptacles are on the same branch.

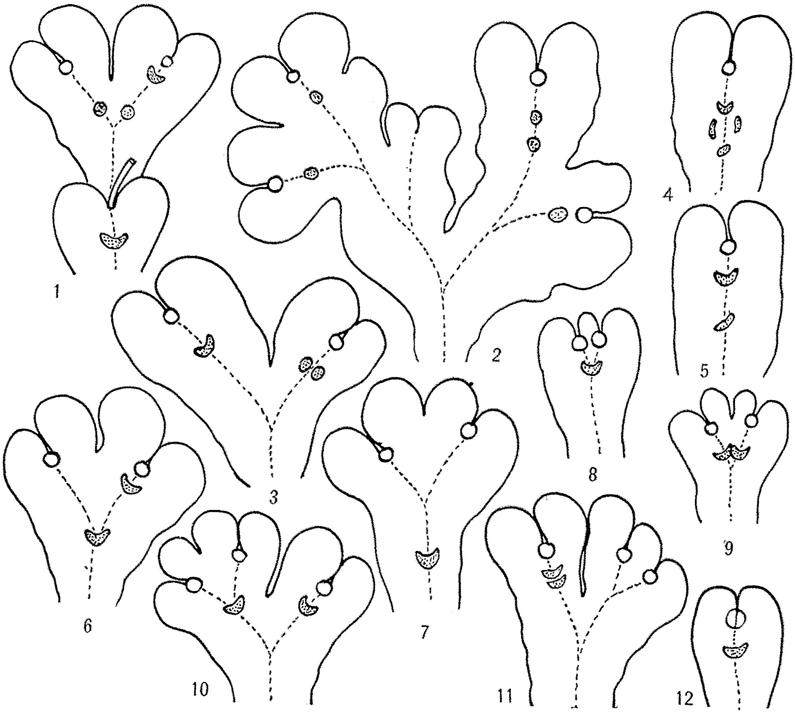
Cavers describes features of Reboulia in several of his papers, giving the only general account of its morphology which we have. He noted (4) the explosive discharge of the sperms, as high as 5 cm. Other phases of Cavers' work will be cited below.

C. and R. Douin (10) review the literature on the "inflorescence" of Reboulia, especially as it relates to the sexual nature of the plant. They credit Boulay (2) as the only observer previous to themselves who has noted marginal male receptacles. They define the antheridial disc as occurring at the end of a ventral or "subfloral" branch, while the female receptacle appears at the tip of an apical branch derived from the former and seeming to be a prolongation of it. They regard this as a distinctive character of Reboulia—"aucun autre genre de Marchantiées ne possède ce caractère." Haupt (16) describes the early antheridium in detail.

## The Male Receptacle

*Position.* The thallus arises as a ventral branch of the previous season's growth, growing out laterally from the midrib or, more commonly, longitudinally from beneath the base of the stalk of the female receptacle, giving a jointed aspect to a two-year plant (fig. 1). The male receptacle occupies a median dorsal position a short distance behind the female receptacle which terminates the branch. Two successive male receptacles are common (figs. 1, 2). Occasionally two discs may be lateral to one another (fig. 3), and rarely a cluster of several discs may be formed (fig. 4). The shoot may form both male and female receptacles without forking (fig. 5), although usually the primary shoot forks from one to three times during a season (fig. 2). The male receptacle may arise before or after the time of forking (compare figs. 1–12). The Douins (10) used the position of the male receptacle as one of the characters in separating from the polymorphic *R. hemisphaerica* of Stephani (26) two new species, *R. occidentalis* and *R. Charrieri*, in both of which the male receptacles are marginal instead of median as in *R. hemisphaerica*. Haupt (16) found a few rare cases of marginal receptacles in this form. The writer has not found a single case in hundreds of plants examined. Haupt thinks there is little justification for the new species. The Douins' claims were based on a careful study of plants grown under similar cultural conditions and can not be set aside summarily.

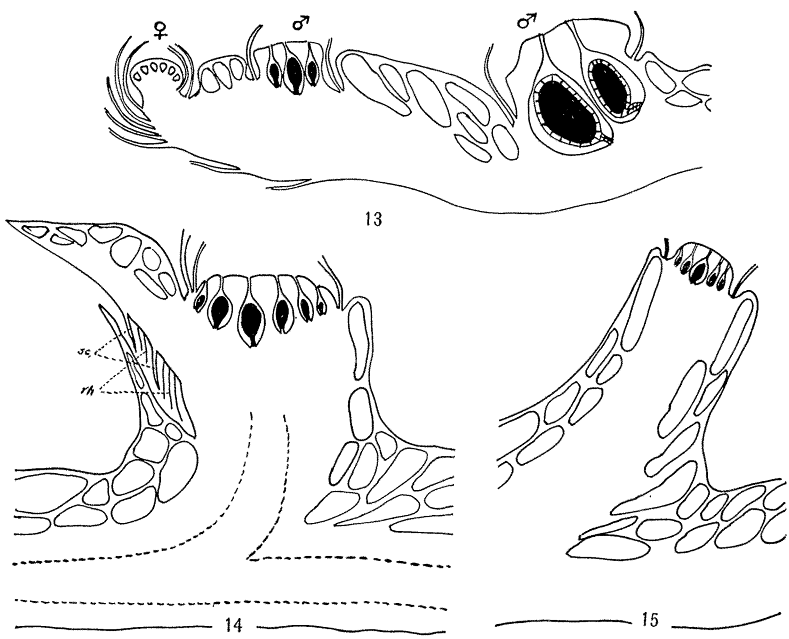
*Form.* In both the proposed new species of Douin the "primary disc" is said to arise as a terminal lunate structure which becomes divided by the growth of the "apical branch" into two circular "secondary discs," these being pushed apart by the widening of the thallus between them and finally coming to occupy a marginal position. The writer has not found




FIGS. 1–12. Habit of the plant of *Reboulia hemisphaerica*, showing the relation of female and male receptacles to one another and to the branching of the thallus. Male receptacles dotted. The dotted line indicates the midrib axis. Figure 1 shows a portion of the previous season's thallus with the base of the stalk of the old female receptacle. × 1.5.

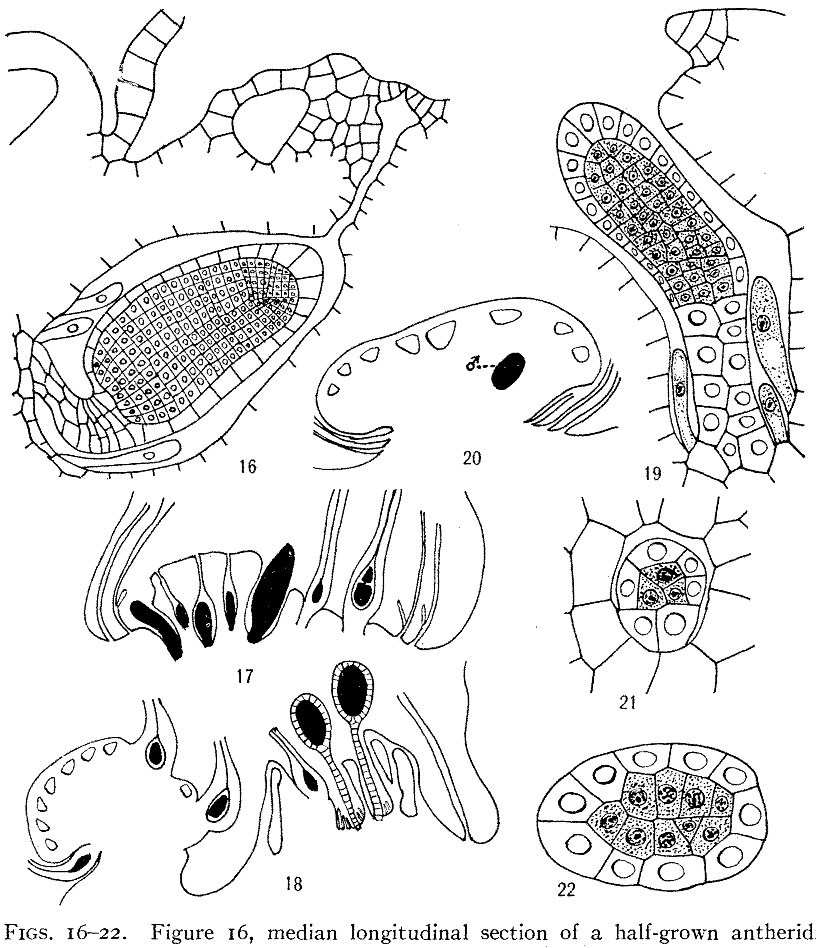
that the later growth of the thallus affects in any way the form of the receptacle, even the lunate disc not being at all correlated with the forking of the thallus (figs. 1, 5, 9, 11). Both oval and lunate discs may occur on the same branch (fig. 1), or two oval (fig. 2) or two lunate discs may succeed one another (fig. 11).

*Structure.* The tissue of the young male disc is rather compact, but with the development of the antheridia the growth of the disc tissue exceeds that of the sex organs which thus become deeply imbedded in deep chambers opening to the exterior by narrow canals and simple air pores (fig. 16). Small air chambers develop between the canals. These chambers have simple pores, so far as found by both Haupt and the writer. Cavers (6) claims small barrel-type openings to occur occasionally. The disc is usually surrounded by a groove within which small narrow scales develop, similar to those around the female receptacle. Mucilage cells arise from the base of the antheridial chamber (figs. 16, 19). Usually the receptacle is raised only a slight distance above the general surface of the thallus (fig. 13), but it may, in some cases, be elevated on a short stalk (figs. 14, 15), the stalk being formed by intercalary growth of the ventral tissue forming a central core surrounded by air-chamber tissue like that of the thallus itself. The fungal hyphae of the compact tissue may penetrate the stalk, and in one case the raised portion bore a few ventral scales and a few pegged rhizoids on the posterior margin (fig. 14).




Figs. 13–15. Vertical longitudinal sections through the receptacles. Figure 13 shows two male receptacles (♂) and the female receptacle (♀), the male receptacles being sessile, as usual. Figures 14 and 15, male receptacle raised on a short stalk. Figure 14 shows the fungus-infected area (indicated by dotted lines) extending into the stalk, as well as small ventral scales (*sc*) and pegged rhizoids (*rh*) on the posterior margin. × 28.

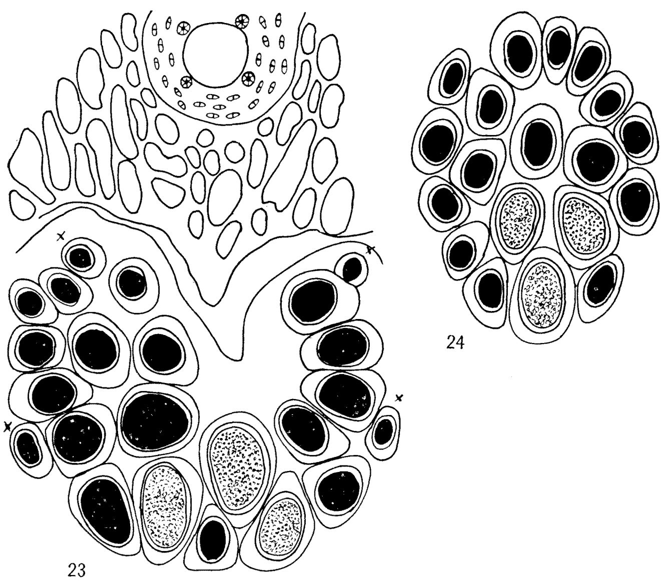
*Bisexual Receptacles.* Bisexual receptacles are not commonly found in the higher Marchantiales. They have been known for a long time in Chomiocarpon (Preissia), where they occur rather frequently, as the writer has found. They were first reported in *Dumortiera irrigua* by Taylor (27), and later for two other species, *D. trichocephala* and *D. velutina*, by Ernst (12). *Monoselenium tenerum*, as reported by Goebel (14), and occasionally certain species of Marchantia, according to Cutting (9), complete the list to date. The writer has found a few such cases in Reboulia, where archegonia may occur on the male receptacle (figs. 17, 18) or antheridia on a female receptacle (figs. 20–22). In the former case some of the antheridia were only partly enclosed by the chamber (fig. 19) or were raised above the surface of the disc by the elongated stalk (fig. 18). The young antheridia




FIGS. 16–22. Figure 16, median longitudinal section of a half-grown antheridium within the antheridial chamber. × 205. Figures 17 and 18, "male receptacles" with archegonia. × 82. Figure 19, young antheridium of figure 17. × 370. Figure 20, "female receptacle" with young antheridium (shown in black). × 82. Figures 21 and 22, young antheridia found in receptacle shown in figure 20. Figure 22 is the detail of the antheridium shown in figure 20. The section was cut obliquely across the antheridium. × 650.

found on the female receptacle were deeply imbedded within the tissue. It is probable that bisexual receptacles will be found in still other forms of the Marchantiaceae, their significance lying in the occasional reversion to a primitive feature, and, as Cavers (8) suggests, they "demonstrate the homology which exists between the male and female receptacles throughout the Marchantiaceae."

*Sexual Nature of the Plant.* Most of the early writers of continental Europe speak of Reboulia as monoecious, occasionally dioecious. On the British Isles, according to both Lett (23) and Cavers (5, 6, 7), it is usually dioecious, occasionally monoecious, in the latter case with the two kinds




FIGS. 23, 24. Transverse sections of male receptacles. Antheridia with mature sperms dotted, immature antheridia black. In figure 23, "*x*" indicates position of the youngest antheridia; female receptacle, with four archegonia, in the apical notch. Air chambers are shown anterior to the male receptacle. × 48.

of receptacles at the apices of different branches, agreeing with the observations of Leitgeb (21, 22). C. and R. Douin (10) claim Reboulia to be autoicous (monoecious), although it may appear dioecious by the abortion of either of the receptacles, but never paroicous. Howe (19) and Haupt (16) both find the American forms to be monoecious. The writer's observations show that the thallus may be sterile, male, female, or bisexual, with both sex organs on different branches or on the same branch, and even in the same receptacle, a variable condition indicating plasticity in this feature.

## The Antheridium

*Origin.* Haupt (16) says that "in all cases the antheridia develop strictly in acropetal succession from segments of the apical cell." The writer finds frequent exceptions to this rule. The first antheridia appear a few segments back of the apical cell and in the development of the receptacle are usually found near the median posterior margin (figs. 23, 24). An examination of the receptacle in transverse and vertical sections shows, however, a tendency toward a centrifugal origin of the sex organs. Young antheridia are found not only lateral, but even posterior to the oldest ones (figs. 14, 15, 23, 24). While, as shown in figure 23, there may be two general strands of sex organs, giving a lunate group, the youngest antheridia occur at the four points marked "*x*," indicating several possible points of origin of the sex organs. The oval disc (fig. 24) is not so definite in points of origin, yet shows a centrifugal development. That this is not merely due to different rates of development is shown by sections of young receptacles (Pl. XIV, figs. 26–29). Figures 26–28 show a young disc in whose development both anterior and posterior apical cells seem to be active, the oldest antheridia being near the center of the disc and the younger ones near the anterior and posterior margins. Oblique sections (fig. 29) and vertical transverse sections of the thallus, through the young disc, show the same condition. While the first antheridia may arise in close connection with the growing point of the thallus, the later ones, especially in a lunate group, may be far removed from the apex of the thallus, arising from apical cells along the margin of the disc (figs. 30, 31).

*Development.* The development of the antheridium, as a general rule, is essentially as given by Haupt (16), the initial arising as a papillate cell (Pl. XIV, fig. 25) which cuts off a basal cell (fig. 28). Other transverse divisions (fig. 29) result in a short filament, usually of four cells (fig. 32)—the limit, according to Haupt, but there may be as many as six (fig. 33), agreeing with the situation in Fimbriaria as described by Campbell (3). Vertical walls usually appear first near the center of the filament (fig. 34), and divide the segments into quadrants (fig. 41). Periclinal walls (figs. 35, 38–40) differentiate the wall from the primary spermatogenous cells. Transverse and vertical divisions of the basal portion build up the stalk (figs. 35, 38–40) which may become comparatively long (fig. 19) and is usually somewhat coiled within the chamber (fig. 16).

In some cases the vertical wall of the terminal cell is strongly inclined (fig. 36). The next wall, cutting at an angle to this, produces an apical cell with two cutting faces from which a few segments may be cut off (figs. 38–40). The writer has also observed this occasionally in Chomiocarpon and Marchantia. This feature suggests the antheridium of Sphagnum and of the Bryales. Inner cells from these segments make their contribution to the spermatogenous tissue (figs. 39, 40, 16). Cross sections of the young antheridia show that in addition to the usual method of differentiation of the wall and primary spermatogenous tissue (figs. 41, 42), interesting variations may occur (figs. 43, 44), in some cases resulting in only two primary spermatogenous cells in the segment and resembling the condition found in the Jungermanniales (fig. 44). Hutchinson (20) showed a considerable variation in the development of the antheridium of *Pellia epiphylla*, both the so-called Marchantia and Jungermannia types occurring. These variations indicate that Reboulia is a plastic form in the development of the antheridium.

The divisions of the primary spermatogenous cells follow no regular plan (figs. 40, 45, 46), although their original boundaries can be detected for a considerable time in the development of the tissue (fig. 16), especially when division takes place, as all the offspring of a primary spermatogenous cell usually divide simultaneously. The wall is a single layer of cells and retains its form until the maturity of the sperms. The young antheridia are somewhat erect, but by the time of maturity have become strongly inclined (figs. 13, 16).

## The Morphological Nature of the Receptacle

There have been two interpretations of the male receptacle of Reboulia. The one, first suggested by Hofmeister (18), regards it as a shoot; the other, put forth by Leitgeb (21, 22), holds it to be merely a dorsal outgrowth. This latter view is based on the claim that the apex of the thallus is not used up in its formation. Even if the thallus is permanently checked, the apex is thought to be evident below the disc. Leitgeb regards the lunate disc as merely a repetition of the form of the thallus notch. Cavers (6, 7), supporting the former idea, says:

> The male receptacle of Reboulia may be regarded as representing a branch, having on its anterior margin a single growing point, or, in many cases, two growing points. Apart from the fact that the branching in the latter case takes place at a late stage, after several antheridia have been formed, and occurs once only, giving rise to a crescent-shaped receptacle, there is no essential difference between the receptacle of Reboulia and that of Fegatella, in which the branching takes place at an earlier stage and is repeated several times, giving rise to radiating rows of antheridia.

He holds the growing point to be used up in the formation of the receptacle, and in some cases to branch, giving the two horns of the disc. The continuation of the thallus in front of the receptacle is regarded as an innovation shoot. Goebel (14) from his study of *Monoselenium tenerum*, a monoecious form with the male receptacle behind the female, which latter may also become dorsally placed, finds that the sessile male disc may be elevated on a short stalk with scales and rhizoids, but without a rhizoid groove. Both receptacles in Monoselenium, according to Goebel, represent branch systems, the antheridia developing in centrifugal order on the upper surface. He regards the forward growth of the thallus as an adventitious branch. From Goebel's claim that the receptacle of a "branch-system" type may become dorsal Cavers (8) concludes that a

> Composite receptacle . . . need not necessarily terminate the growth of the thallus but may come to occupy the same position as the "dorsal outgrowth" type of receptacle which Leitgeb regarded as contrasting so strongly with the "branch-system" type.

Goebel (14, 15) would explain the dorsal sessile receptacles, such as occur in Reboulia and Plagiochasma, as reduced from those of forms such as

Marchantia and Chomiocarpon, the dorsal position being due to the very early appearance of the adventitious branch. The male and female receptacles, according to this, are morphologically equivalent, Goebel holding that receptacles of different morphological nature are improbable on the same plant. Voigt (28), Leitgeb (21, 22), and Cavers (7) all found female receptacles in Reboulia in a median dorsal position behind the apex, conditions giving support to the homology of the two receptacles, despite the abnormality of such a position of the female receptacles. Evans (13), discussing the homology of the female receptacle in Plagiochasma and Reboulia, says:

> The mere fact that the growing point is not carried upward by the elongating stalk (in Plagiochasma) does not invalidate the homology of the carpocephalum with that of Reboulia.

His conclusion could be applied to the male receptacle as well. Haupt (16) finds the activity of the apical cell unchecked in the formation of the disc and apparently holds to Leitgeb's view.

It was shown above that the disc may be elevated on a short stalk which may, in rare cases, bear scales and pegged rhizoids. The presence of one or more growing points on the young receptacle is evident, as well as is the formation of apical cells on the disc independent of the apex of the thallus (fig. 30). The writer is inclined to the view that in the male receptacle of Reboulia we have a possible elementary stage of a branch system, representing a transition from the "dorsal outgrowth" to the "composite" form, or *vice versa* if one were to insist on a reduction series. Reboulia is sufficiently plastic to give several phases of the transition, as, for example: the thallus apex may be unchecked, the sessile male receptacles frequently dorsal, the female receptacle occasionally dorsal; the growth of the thallus may be checked temporarily by the formation of the male receptacle, an innovation shoot growing out with a narrow base, giving the jointed aspect of the plant sometimes figured, as by Goebel (15); the thallus apex may be permanently checked, being used up in the formation of the male receptacle, which remains as a sessile structure (as in Lunularia and Conocephalum); and, rarely, the male receptacle may be elevated on a short stalk (figs. 14, 15). The marginal male receptacles, as found by C. and R. Douin (10), and the occasional clusters (figs. 3, 4) can be explained as due to intercalary growth following the forking of the disc, thus separating the several points of origin from one another.

## Conclusion

On the whole it seems to the writer that the male receptacle and the antheridium of Reboulia suggest a very plastic and significant condition from a morphological standpoint, being primitive in some features and suggestive of higher forms in others.

## Summary

1. The male receptacle of *Reboulia hemisphaerica* occupies a dorsal position, as a rule, posterior to the female receptacle which terminates the branch.

2. The receptacle is usually more or less lunate in outline, although it may be circular, or more or less irregular. It is sessile, as a rule, although in rare cases it may be elevated on a very short stalk.

3. *R. hemisphaerica* is monoecious, with the sex organs in distinct groups, although bisexual receptacles may occur.

4. The antheridia show a tendency toward centrifugal development. Variations from the usual marchantiaceous type of development occur, such as the occasional appearance of an apical cell with two cutting faces and the occasional formation of only two primary spermatogenous cells in a segment.

5. The male receptacle is a plastic structure, probably representing an elementary stage of a branch system and showing transitions from the "dorsal outgrowth" type to the "composite branch-system" type.

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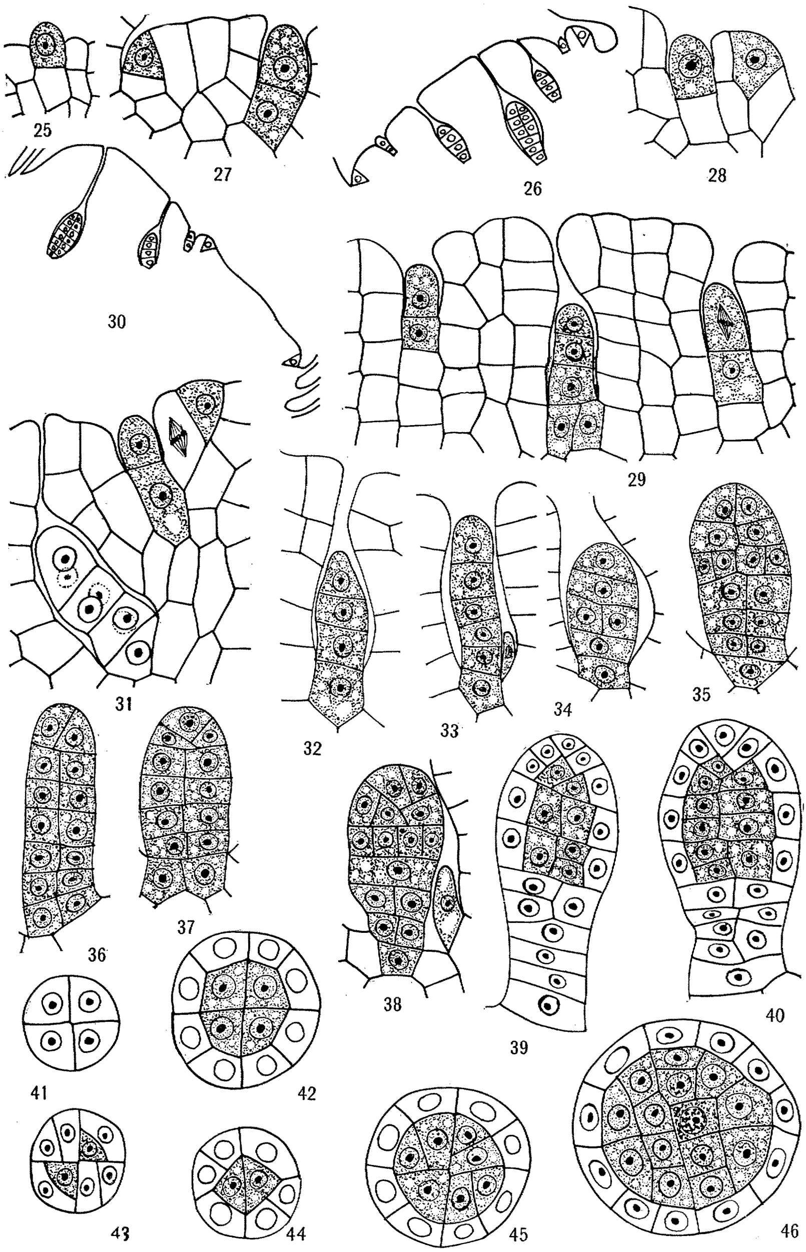


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## EXPLANATION OF PLATE XIV

All drawings were made with a camera lucida and have been reduced one half in reproduction.

FIG. 25. Antheridium initial. × 650.

FIG. 26. Section of a young male receptacle, showing the centrifugal development of antheridia. × 155.

FIGS. 27, 28. Detail of the anterior and posterior margins, respectively, of figure 26; figure 28 shows antheridium initial; figure 27, basal cell cut off. × 650.

FIG. 29. Portion of a receptacle showing younger antheridia on either side of the older one. × 650.

FIG. 30. Section of a young receptacle with an apical cell at the anterior margin of the disc, some distance posterior to the apical cell of the thallus. × 155.

FIG. 31. Detail of a portion of figure 30. × 650.

FIGS. 32–35. Development of young antheridia. × 650.

FIGS. 36–40. Young antheridia with apical cell of two cutting faces. × 650.

FIGS. 41–46. Transverse sections of young antheridia. × 650.